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CHAPTER 16-3
BIRD NESTS

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Figure 1. Nest with mosses, lichens, and baby birds. Photo by Kytka through public domain.

Nests

Within a thick and spreading hawthorn bush
That overhung a molehill large and round,
I heard from morn to morn a merr thrush
Sing hymns of rapture, while I drank the
Sound with joy – and oft an unintruding guest,
I watched her secret toils from day to day;
How true she warped the moss to form her nest,
and modell'd it within with wood and clay.

The Thrush's Nest, by Claire
(in Marshall 1908)

Nests are complex structures that often consist of structural differences within a single nest. Most bird nests occur in unique habitats and are constructed of specific materials (Heinrich 2000). The nests themselves are typically so unique that the owner/builder can be identified by the nest. In some cases, false nests are built by the male to discourage would-be suitors from enticing the female away.

The greatest vulnerability in the life cycle is typically during the time the young birds are in the nest (Heinrich 2000). Thus the construction and location of the nest are important survival factors (Heinrich 2000; Mainwaring *et al*. 2012). Most nests are built by the females, but in some cases it is the male who builds the nest(s), using them as sex attractants (Heinrich 2000). But the female typically chooses the site.

Although many nests are built for one-time use by the builder, some nests are reused by the same bird or by other animals for other purposes (Heinrich 2000). For example, the deermouse climbs the tree to find a bird nest, then relocates it near the ground and fills it with seeds to store for the winter.

The importance of bryophytes in the Antarctic is illustrated at Vestfold Hills, East Antarctica. There was greater species diversity of mosses and lichens in sites

adjacent to nests than away from them. Is this a **guano** (bird droppings) benefit to the bryophytes, a moisture or insulation benefit to the birds, or a combination of both? Or do the bryophytes simply like the same locations as the birds? Soil nutrients were not significantly associated with moss diversity or abundance. Rather, both species and abundance of mosses have a positive association with soil water content. So it may be that the birds prefer nesting sites that are also preferred by the mosses.

Types of Nests

Wikipedia (2017) defines nine types of nests. The most common and familiar of these is the **cup** nest that is the product of many of the passerine birds.

The **scrape** nest (Figure 2) is the simplest. It is merely a depression in the soil or vegetation, but it may benefit from the addition of materials, such as bits of vegetation, small stones, shell fragments, or feathers. Mosses may form the base of such a nest. It usually has a rim to prevent eggs from rolling away. This type of nest is the most exposed, thus offering the least protection. This nest style is used by ostriches, many kinds of ducks, most shorebirds, most terns, some falcons, pheasants, quail, partridges, bustards, and sand grouse.

Figure 2. The **scrape** nest of ***Charadrius*** sp., a plover. This nest is lined with shells to support the eggs when the soil or sand become muddy. Photo by Gniazdo Sieweczki RB, through Creative Commons.

The **mound** nest (Figure 3) is typically made of soil, branches, sticks, twigs, and/or leaves (Wikipedia 2017). The females lay their eggs within the mounds, and the rotting vegetable matter generates heat that helps to warm and incubate the eggs. The largest of these nests is that of the Australasian megapodes. In some cases, as in the Australian Brush Turkey (*Alectura lathami*), the gender of the hatched eggs is affected by the temperature, with more females at higher temperatures (Göth 2007). Others building mound nests include the horned coot and the flamingo (Wikipedia 2017).

Figure 3. Malleefowl **mound** nest. Photo by Glen Fergus, through Creative Commons.

The **burrow** is an underground excavation that may be created by the bird or repurposed from a previous mammalian or tortoise owner (Wikipedia 2017). These are sometimes lined with mosses and usually have a tunnel entrance to an egg chamber. The bird occupants include white-browed tits, puffins, shearwaters, some megapodes, motmots, todies, most kingfishers, the crab plover, miners, and leaftossers.

Figure 4. The Sand Martin, *Riparia riparia*, in **burrow** nest. Photo by Bruce, through Creative Commons.

The **cavity** nest (Figure 5) is built in living or dead wood, tree ferns, or some cacti (Wikipedia 2017). The **cavity** nester is more likely to use bryophytes than the above-named nest builders. These are used to line the cavity and to elevate the base to a suitable height for entering and feeding the young birds. Some of the birds excavate their own cavities (woodpeckers, trogons, some nuthatches, many barbets). But far more species (parrots, tits, bluebirds, most hornbills, some kingfishers, some owls, some ducks, some flycatchers) must find holes already large enough.

Figure 5. *Dryocopus martius* (Black Woodpecker) with its **cavity nest**. Photo by Alastair Rae, through Creative Commons.

When most people think of a bird nest, it is the **cup** nest (Figure 6) that they visualize. These nests are open from the top and smoothly hemispherical inside, with a deep depression to house the eggs (Wikipedia 2017). The materials used are mostly pliable and some species specifically use bryophytes, either in the construction, the lining, or the outermost layer – perhaps as camouflage. The nest mass often correlates with the weight/size of the adult bird it must support. The insulation quality of the nest relates to nest mass, nest wall thickness, nest depth, nest weave density and porosity, surface area, height above ground, and elevation above sea level. Among the many cup builders are the robin and the tiny hummingbird. Some are attached to the branch with saliva, and some hummingbirds use spider webs to affix the nest.

Figure 6. ***Passerculus sandwichensis***, Savannah Sparrow **cup** nest. Photo by Kati Fleming, through Creative Commons.

The **saucer** or **plate** nest is somewhat similar to the cup nest, but has very little, if any, depression (Wikipedia 2017). This nest may be within the range of nest variation for a cup builder.

The **platform** nest (Figure 7) is large and flat. It is occasionally lined with mosses (Wikipedia 2017). This nest type is common among some ducks and birds of prey. This more permanent structure can be used y the same pair of birds for many years.

Figure 7. Osprey (*Pandion haliaetus*) and **platform** nest. Photo by Tibor Duliskovich, through Creative Commons.

The **pendant** nest (Figure 8) is an elongated sac that hangs from a branch (Wikipedia 2017). Pendant nest builders include Oropendolas, caciques, orioles, weavers, and sunbirds. Some of these birds construct their nests from bryophytes.

Figure 8. ***Ploceus castaneiceps*** (Taveta Golden-weaver) **pendant** nest. Photo by Robert Lawton, through Creative Commons.

The **sphere** nest (Figure 9) is a globe-shaped nest that is completely enclosed except for a small opening which may be near the bottom (Wikipedia 2017).

Figure 9. Weaver (**Ploceidae**) on **sphere** nest. Photo by Bernard Dupont, through Creative Commons.

Bryophyte Advantages in Bird Nests

Use of mosses for bird nests is not uncommon. Annie Martin (Bryonet 1 June 2010) reports that as many as forty different types of birds use mosses in constructing their nests. While that may be a local number, many more examples are known worldwide. Birds have long been recognized as consumers of mosses and liverworts for nesting materials (Figure 10) (Takaki 1957, Breil & Moyle 1976 – SE USA; Takeshita 1978, Furuki & Onuma 1996 – Japan; Hribek 1985 – Europe; Abolina 1991 – Lithuania; Cao & Caihua 1991, Cao *et al*. 2010 – China), to name a few. Richardson (1981) listed 53 British birds that use mosses to some degree in their nests; Campbell and Ferguson-Lees (1972) reported 52 from that region. Jadin and Billiet (1979) described the activities of birds building nests with mosses and liverworts on Reunion Island in the Indian Ocean.

Figure 10. Cup nest made of leafy liverworts in Costa Rica. Photo courtesy of Dave Fenlon.

Birds and bryophytes can have close relationships that permit both of them to reproduce. Some birds have an incessant need to make nests, and mosses can be a favorite building material. I found it impossible to develop any kind of moss garden in my garden room when it housed 10 Zebra Finches (***Taeniopygia guttata***; Figure 11) because within days or even hours every scrap of the moss had been moved from my chosen location to the midst of the bamboo clump, where it aided in forming massive 3-story apartment nests. I ultimately had to get rid of the finches and traded them for Society Finches, birds that have a little more reverence for mosses and don't find nest building to be an essential daily activity!

Figure 11. ***Taeniopygia guttata***, Zebra Finch, a bird that often uses mosses in its nests, at least when choices are limited. Photo by Peripitus, through Creative Commons.

The families of birds using mosses to some degree in their nests ranges widely. We need consider only a few examples to illustrate this. In the **Passeriformes**, Hribek (1985) found that among others in the **Paridae**, the Great Tit (***Parus major***; Figure 18-Figure 19) and the Blue Tit (***Cyanistes caeruleus***; Figure 22) use mosses in their nests, as does the Pallas Dipper (***Cinclus pallasii***; Figure 12) in the **Cinclidae** (Nishimura *et al.* 1980). In the **Apodiformes: Apodidae**, the Philippine Swiftlet (***Aerodramus mearnsi***; Figure 13) uses bryophytes (Tan *et al*. 1982). In the **Podicipediformes: Podicipedidae**, breeding populations of the Red-necked Grebe (***Podiceps grisegena***; Figure 14-Figure 15) in the Northwest Territories use ***Sphagnum*** (Figure 16) in addition to cattails and other emergent vegetation in nest construction (Fournier & Hines 1998). Even the huge American Bald Eagle (***Haliaeetus leucocephalus*** in the **Falconiformes: Accipitridae**; Figure 17) in Alaska uses mosses in old-growth forests in their nests atop tall spruce trees (Holleman 1997).

Figure 12. ***Cinclus pallasii***, Brown dipper, Pallas Dipper, in stream. This species collects aquatic mosses to make its nest. Photo by Alpsdake, through Creative Commons.

Figure 13. ***Aerodramus mearnsi***, Philippine Swiftlet, with its challenging moss nest. Photo by Angie Cederlund, with permission.

Figure 14. ***Podiceps grisegena***, Red-necked Grebe with ducklings, a species that uses mosses in its nest. Photo through public domain.

Figure 15. ***Podiceps grisegena***, Red-necked Grebe, on its nest with nestlings on its back. Photo by Lukasz Lukasik, through Creative Commons.

Figure 16. ***Sphagnum fimbriatum***; ***Sphagnum*** is used as a nest material for the Red-necked Grebe. Photo by James K. Lindsey, with permission.

Figure 17. ***Haliaeetus leucocephalus***, American Bald Eagle landing on nest. This species uses mosses in building its nest in Alaska. Photo by Murray Foubister, through Creative Commons.

With such a large number of birds using bryophytes in their nests, we must ask why? Do they provide some special attributes that make them desirable? Or are they simply easy to collect and available?

Alabrudzińska *et al*. (2003) found that the quantity and proportion of mosses in nests and the nest size can influence the success of eggs as well as of the nestlings, as seen in the Great Tits (***Parus major***; Figure 18-Figure 19). They considered that nest size and composition must satisfy contradictory pressures needed for survival. The nest must be kept moist with a relatively constant temperature. It must also protect the eggs and young from predation and limit disease and parasites.

Figure 18. ***Parus major***, Great Tit male, a bird that includes mosses in its nest. Photo by Charles J. Sharp, through Creative Commons.

Figure 19. ***Parus major*** nest with moss, down, and nestlings. Photo by Notts Ex Miner, through Creative Commons.

Insulation

Bryophytes can have beneficial effects that are not provided by other nesting materials. Providing insulation may be the first use that comes to mind. Birds often use grasses, feathers, and fur to regulate the nest temperature (Bartholomew *et al.* 1976; Winkler 1993; Blem & Blem 1994; Lombardo *et al.* 1995), much as we put on a winter coat or sleep under a quilt. But bryophytes can provide insulation as well.

Several studies have indicated the importance of nest temperature. Olson *et al*. (2006) used Zebra Finches (***Taeniopygia guttata***; Figure 11) to evaluate the importance of temperature on embryo development. They found that after 12 days of incubation, periodic cooling resulted in lower embryo mass and yolk reserves compared to controls incubated at 37.5ºC. When the eggs were cooled to 20ºC regularly, the embryos had higher mass-specific metabolic rates and delayed development.

Peréz *et al*. (2008) experimentally heated the nests of the Tree Swallow (***Tachycineta bicolor***; Figure 20) during incubation. They found that incubating females maintained better body condition and fed nestlings at a greater rate. Their nestlings similarly had higher body mass and better body condition. In contrast, Ardia *et al*. (2008) examined the effects of cooling on the same species. They found that cooled eggs required longer incubation periods and the nestlings had a lower immunity to bacteria. Embryos that were exposed to experimental cooling resulted in nestlings that had lower residual and absolute body mass. The cooled females made fewer feeding trips, but this seemed to have no effect on nestling immunity to bacteria.

Figure 20. ***Tachycineta bicolor***, Tree Swallow, a species in which nest temperature affects health of the nestlings. Photo by John Benson, through Creative Commons.

One means by which birds can alter the temperature of a nest is by increasing its size or thickness. This mechanism is used by the Great Tit, ***Parus major*** (Figure 18-Figure 19) (Alabrudzińska *et al*. 2003). Clutch size (Figure 21) correlates negatively with total nest mass, but is positively correlated with the proportion of nest mass in the lining. Successful performances of eggs and nestlings are attributable to the quantity and proportion of moss in the nest structure as well as the nest size. Alabrudzińska and coworkers suggest that nest size and composition may affect moisture, temperature, protection, and/or sanitary conditions of the nest, thus supporting the hypothesis that mosses serve as more than structural materials.

Figure 21. ***Parus major***, Great Tit, nest with moss and eggs in nest box. Photo by Notts Ex Miner, through Creative Commons.

Deeming *et al*. (2012) extended this study to determine what triggers affect usage of more mosses in the nests of the Blue Tits (***Cyanistes caeruleus***; Figure 22) and Great Tits (***Parus major***; Figure 18-Figure 19, Figure 21). They found that nest mass is inversely related to temperatures experienced by the female during nest construction. Nest cup mass in particular is related to the temperatures experienced by the females during the seven days prior to the beginning of egg laying. This behavior is independent of latitude (Deeming *et al*. 2012), but nests are heavier at higher latitudes (Mainwaring *et al*. 2012).

Figure 22. ***Cyanistes caeruleus***, Blue Tit adult, feeding. Photo by Dave Howes, through Creative Commons.

The Sociable Weaver (***Philetairus socius***; Figure 36-Figure 37) can serve to illustrate the role nesting materials might play and give us some insight into the role mosses could play. The nest of the Sociable Weaver consists of multiple chambers, and in summer each chamber is occupied by 1-2 birds, whereas in winter there may be up to 5 birds in a chamber, with some chambers remaining empty (Bartholomew *et al.* 1976). Bartholomew and coworkers found that for the Sociable Weaver in the Kalahari Gemsbok National Park, South Africa, the nest temperatures varied only 7-8ºC when the outside temperatures ranged from 16-33.5ºC. This temperature is controlled largely by the number of birds in a chamber. Van Dijk *et al.* (2013) further found that nest volume had no effect on its thermoregulatory benefits. Nevertheless, the central part of the nest had the most stable conditions.

Blem and Blem (1994) suggested that the moist bryophytes could alter the nest temperature, presumably cooling it through evaporative cooling, and certainly maintaining a cool temperature longer against the hot (~43ºC) body temperature of the birds, much like a runner putting a wet band around his or her head. On the other hand, I suggest that the dark-colored mosses can also absorb sunshine like a dark body and warm the nest on cool days before leaves appear on the trees.

The nest of the **Prothonotary Warbler** (***Protonotaria citrea***; Figure 23), a cavity nester, consists of a cup made of grasses, leaves, and rootlets placed on a thick mat of moist, green bryophytes – both mosses and liverworts (Bent 1953; Petit 1989; Blem & Blem 1992). These bryophytes remain moist during the incubation and nestling stages (Blem & Blem 1994). It is likely that this nest composition affects the nest living conditions (Mertens 1977 a, b). The bryophyte composition of these nests ranges 74.7-80.2% of the dry mass of the nest. ***Anomodon attenuatus*** (Figure 24) is the most used of the five moss and two liverwort species. The other bryophytes found in nests were the mosses ***Haplocladium microphyllum*** (Figure 25), ***Amblystegium varium*** (Figure 26), ***Plagiomnium cuspidatum*** (Figure 27), and ***Thuidium delicatulum*** (Figure 28), and the liverworts ***Porella platyphylla*** (Figure 29) and ***Frullania eboracensis*** (Figure 30). The woven bryophyte nest is also able to expand as the baby birds grow, maintaining a tight fit to the tiny eggs, but expanding as the young birds grow.

Figure 23. ***Protonotaria citrea***, Prothonotary Warbler, a species that builds its nest on a mat of moist, green mosses. Photo by William H. Majoros, through Creative Commons.

Figure 24. ***Anomodon attenuatus***, a pleurocarpous moss used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Michael Lüth, with permission.

Figure 25. ***Haplocladium microphyllum***, a pleurocarpous moss used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Robin Bovey, with permission through Dale Vitt.

Figure 26. ***Amblystegium varium***, a pleurocarpous moss used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Michael Lüth, with permission.

Figure 27. ***Plagiomnium cuspidatum***, a plagiotropic moss used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Michael Lüth, with permission.

Figure 28. ***Thuidium delicatulum***, a pleurocarpous moss used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Janice Glime.

Figure 29. ***Porella platyphylla***, a leafy liverwort that grows on rocks and trees and is used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Tim Waters through Creative Commons.

Figure 30. ***Frullania eboracensis***, a leafy liverwort that grows on bark and is used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Robert Klips, with permission.

Most of the evidence of the importance of bryophytes as insulators is inconclusive. Mainwaring *et al*. (2012) found that insulative properties of nest linings decreased as

the season progressed. The Blue Tit (***Cyanistes caeruleus***; Figure 22) exhibited seasonal changes in the nest composition, but the mass of mosses in the base of the nest showed no seasonal variation (Mainwaring *et al*. 2014). On the other hand, there was a seasonal decline in the mass of materials used to line the cup (Mainwaring & Hartley 2008).

Deeming and Mainwaring (2015) found that the Blue Tits (***Cyanistes caeruleus***; Figure 22), European Pied Flycatchers (***Ficedula hypoleuca***; Figure 31), and Common Redstart (***Phoenicurus phoenicurus***; Figure 32) used different nesting materials in the same types of nest boxes. Blue Tits used mostly mosses with hair, fur, and feathers (Figure 33); Flycatchers used leaves and grass (Figure 34); Redstarts used leaves, grass, moss, and lots of feathers. (Figure 35). Nevertheless, all three nest types have similar insulating properties.

Figure 31. ***Ficedula hypoleuca***, European Pied Flycatcher, a non-moss user. Photo by Ron Knight, through Creative Commons.

Figure 32. ***Phoenicurus phoenicurus***, Common Redstart, with earwig; this species uses mosses and other materials. Photo by Yerpo, through Creative Commons.

Figure 33. ***Cyanistes caeruleus***, Blue Tit, nest with mosses, feathers, and hair. Photo by Arnstein Ronning, through Creative Commons.

Figure 34. ***Ficedula hypoleuca***, European Pied Flycatcher, eggs with leaves and grass in the nest; mosses are not used. Photo by Arnstei Rønning, through Creative Commons.

Figure 35. ***Phoenicurus phoenicurus***, Common Redstart nest with moss, grasses, feathers, and eggs. Photo by Roberto Zanon, through Creative Common.

Humidity Control

Humidity control can be important for young birds, and nest materials can be used to buffer changes in humidity. We can use the Sociable Weaver (***Philetairus socius***; Figure 36) once more to illustrate this role, perhaps in the extreme.

Figure 36. ***Philetairus socius***, Sociable Weaver, a bird that builds a huge apartment nest that regulates humidity. Photo by Charles J. Sharp, through Creative Commons.

The Sociable Weaver (***Philetairus socius***; Figure 36) builds the largest bird nest (Figure 37) on the planet (van Dijk *et al*. 2013), housing at times over 100 pairs of birds (White *et al*. 1975). The nest is usually constructed in trees, using large twigs to construct the roof (Sociable Weaver 2017). Dry grasses separate the chambers and sharp spikes of straw deter predators from traversing the entrance tunnels. Inside, soft plant material, fur, cotton, and fluff line the nesting chambers. I can't help but wonder if bryophytes would be included if they were available in its habitat.

For the Sociable Weaver, the nest materials absorb the humidity, maintaining a lower humidity than that in the outside air (Bartholomew *et al.* 1976). The Sociable Weaver (***Philetairus socius***; Figure 36) does not use bryophytes, probably due to scarcity in its dry habitat, but where the bryophytes grow and are used by birds, I would expect them to have a significant role in absorbing and retaining humidity. I have taken bryophytes from a desiccator and watched their weight rise as I tried to weigh them. Bryophytes are able to take moisture out of the atmosphere, and thus they could also absorb moisture created by the birds' bodies. On the other hand, when the atmosphere is dry, the bryophytes could absorb moisture at night and help to keep baby birds, with scant covering of feathers, from drying out during the day.

Wimberger (1984) noted that the use of fresh bryophytes raised the humidity in nest cavities. This could prevent egg desiccation and increase hatching success (see also Clark & Mason 1985). On the other hand, the Fieldfare (***Turdus pilaris***; Figure 38-Figure 40) has an open nest, using grass and mud with very little moss or lichen. Compared to other species, the Fieldfare lost water rapidly. Within 10 minutes of removal of a water source, only 54% humidity remained in the nest, whereas the Redwing (***Turdus iliacus***; Figure 41) nest had 66%, the Eurasian Blackcap (***Sylvia atricapilla***; Figure 42-Figure 44) 71%, the Pied Flycatcher (***Ficedula hypoleuca***; Figure 31, Figure 34) 73%, the Chaffinch (***Fringilla coelebs***) 80%, and the Brambling (***Fringilla montifringilla***) 81%. Thrushes (**Turdidae**) made dense nests that still contained considerable water several days later. When the water content of the mosses and lichens was increased from 30% to 60%, the water content of the nest 24 hours later rose from 27% to 41%.

Figure 37. The very large nest of ***Philetairus socius***, Sociable Weaver. Photo by Harald Süpfle, through Creative Commons.

Figure 38. ***Turdus pilaris***, Fieldfare, with worm. This species uses little or no moss in its nest and the nest loses water rapidly. Photo by Grzegorz Golebiowski, through Creative Commons.

Figure 39. ***Turdus pilaris***, Fieldfare fledgling. Photo by Ernst Vikne, through Creative Commons.

Figure 40. ***Turdus pilaris***, Fieldfare, babies in nest – a species that uses few or no mosses in its nest. Photo by Arnstein Rønning, through Creative Commons.

Figure 41. ***Turdus iliacus***, Redwing, a bird that builds a nest that maintains moisture. Photo by Steve Garvie, through Creative Commons.

Figure 42. ***Sylvia atricapilla***, European Blackcap. Photo by S. Drozd Lund, through Creative Commons.

Figure 43. ***Sylvia atricapilla***, European Blackcap, a nest that is able to hold moisture. Photo by James K. Lindsey, with permission.

Figure 44. ***Sylvia atricapilla***, Eurasian Blackcap, nest with nestlings. Photo through Creative Commons.

Fontúrbel *et al*. (2020) noted that hummingbirds benefit from moisture retention by mosses, preventing eggs from drying out (see also Breil & Moyle 1976; Blem & Blem 1994).

In a study on passerine birds, Slagsvold (1989b) found that the width of the interior of the nest cup correlated negatively with the amount of mosses and lichens used in construction. It would seem, then, that using more mosses and narrowing the interior of the nest would provide a more insulated, more moist environment, and that bryophytes can be major contributors to those effects.

Elasticity

Elasticity can be important for both insulation and humidity. Slagsvold (1989a) noticed that the Chaffinch (***Fringilla coelebs***; Figure 45-Figure 46) and Brambling (***Fringilla montifringilla***; Figure 47) construct nest cups that expand in proportion to the number of young. This would also permit the nest to expand as the nestlings grow, continuing to maintain a warm blanket effect around them.

Slagsvold (1989a) considered selection for elastic nesting materials such as mosses and lichens as important criteria. But it appears that it is the ability to absorb rainwater rapidly, then to dry slowly, that is important.

Among the passerine birds, Slagsvold surmised that narrow nest cups were especially common with small-sized birds that nest above ground. These nests are typically open and include large quantities of mosses and lichens.

Figure 45. ***Fringilla coelebs***, Chaffinch, a bird that selects nesting materials, such as bryophytes, that expand as nestlings grow. Photo by Andreas Trepte, through Creative Commons.

Figure 46. ***Fringilla coelebs***, Chaffinch, expandable nest with mosses. Photo by Trachemys, through Creative Commons.

Figure 47. ***Fringilla montifringilla***, Brambling male, a species for which mosses keep the nest moist. Photo by M. M. Lolek, through Creative Commons.

Antibacterial, Antiparasitic?

There are lots of hungry predators, albeit tiny, that enjoy living on birds. These can take a toll on survival. Adults and juveniles of the Cliff Swallow (***Petrochelidon pyrrhonota***; Figure 48) occupying parasite-free (fumigated) colonies had an average of 4.4% (adults) and 62.2% (juveniles) greater daily survival than their counterparts in naturally infested colonies (Brown & Brown 2004). Several researchers (Wimberger 1984; Clark & Mason 1985) suggest that the bryophytes may serve as insecticidal and anti-pathogenic agents in the nest. Clark and Mason examined the European Starling (***Sturnus vulgaris***; Figure 49) as a likely recipient of such help because it uses the same nest for multiple years, thus increasing the chances for parasite and pathogen encounter. This species chooses fresh green material in its nest, restricting its selection to a small number of species and choosing plants with volatile compounds that are likely to inhibit arthropod hatching or bacterial growth. These plants typically possess greater concentrations of mono- and sesquiterpenes than the local flora in general.

Figure 48. ***Petrochelidon pyrrhonota***, Cliff Swallow, a bird that has lots of parasites. Photo by Ingrid Taylar, through Creative Commons.

Figure 49. ***Sturnus vulgaris***, European Starling, a species that re-uses its nest and incorporates plants that contain greater concentrations of mono- and sesquiterpenes than the local flora in general. Photo by Luzmaria, through Creative Commons.

Igic *et al*. (2009) found that the Song Thrush (***Turdus philomelos***; Figure 50) used cigarette butts in its nest (Figure 51). This raised the question of anti-predatory nesting materials, as shown by Strecker (1926) and Schuetz (2005) for shed snake skins and carnivore scat. But mosses and odiferous leaves may serve this function as well, protecting birds against ectoparasites (Clark & Mason 1988; Banbura *et al*. 1995; Lambrechts & Santos 2000).

Figure 50. ***Turdus philomelos***, Song Thrush, a bird that may use anti-predatory nesting material. Photo by Yvan, through Creative Commons.

Figure 51. ***Turdus philomelos***, Song Thrush, feeding babies in New Zealand nest. Photo from ZipCodeZoo, through Creative Commons.

Blue Tits (***Cyanistes caeruleus***; Figure 22) use odor cues to determine when to replace green plant materials (Mennerat 2008). The female Blue Tits bring fresh plants to their nests (Banbura *et al*. 1995), so there is reason to believe that these plants may be chemically endowed in a way that helps to protect the nest. Both parents hesitated longer before entering the nest box when the experimenter added green tracheophyte material compared to addition of mosses. Banbura concluded that we cannot rule out antiparasite functions of green plant material in the Blue Tit nests, but neither can we say conclusively that they serve this purpose.

On Corsica, Mennerat *et al*. (2009a, b) found that despite adding aromatic plants to their nests, the Blue Tit (***Cyanistes caeruleus***; Figure 22) experiences just as many parasites as without them. However, their growth is improved. The researchers found that the bacterial community in the nest was significantly affected by these plants, being reduced on nestlings. This offered the further advantage that the bacteria reduced most on the chicks with the worst infestations of the blood-sucking blowfly larvae (*Protocalliphora*). On the other hand, birds in nests where aromatic plants were replaced by mosses did not experience the benefits experienced in accompaniment of the aromatic plants: chick mass gain, higher haematocrit levels, faster feather development (Mennerat *et al.* 2009b).

Shutler and Campbell (2007) added greenery to nests of the non-greenery-using Tree Swallows (***Tachycineta bicolor***; Figure 20). They found no evidence that feathers had reduced parasites, but the added green plant material did result in lower numbers of ectoparasites in the nests. Nevertheless, there was no increase in breeding success.

Dawson *et al*. (2011) investigated the use of feathers to line nests in the Tree Swallow (***Tachycineta bicolor***; Figure 20). They found that adding feathers to nests actually increased the abundance of ectoparasites in those nests, a conclusion previously noted by Lombardo *et al.* (1995). Dawson and coworkers interpreted this to mean that the feathers separated the nestlings from the parasites. This conclusion supported that of Winkler (1993) in a study that showed that removal of feathers from Tree Swallow nests caused higher mite and lice infestation on nestlings, coinciding with lower growth rates of the nestlings, compared to controls. But there is also a cost to males that spend more time to gather more feathers – they are more likely to lose their mate to another male!

Wimberger (1984) further showed that birds in **Falconiformes** that used their nests in successive years were more likely to include green foliage, including bryophytes, than those species that did not reuse their nests. This suggests that the bryophytes may have some sort of protective function.

If birds choose nesting materials based on their antibiotic properties, it would seem that they would need to detect the odors caused by the compounds that facilitate this antibiotic use. But the **Passeriformes** (the birds that more often use bryophytes in their nests) are known to have a very small relative **olfactory** (odor-sensing) bulb size (Mennerat *et al*. 2005). Thus we have assumed that these birds have poor olfactory senses.

It appears that this wisdom is misleading, at least for some passerine birds (Mennerat *et al*. 2005; Strandh *et al.* 2012). The Blue Tit (***Cyanistes caeruleus***; Figure 22) uses mosses in her nest and this species is one of the birds that is sensitive to the odor of lavender (Mennerat *et al*. 2005). If birds choose vegetation based on the odor of volatile compounds, then I am surprised that the aromatic thallose liverworts do not seem to be used in nests.

Brian Dykstra (pers. comm. 10 December 2011) asked an interesting question. Liverworts such as species of ***Frullania*** (Figure 30) often house rotifers in their lobules (Figure 52). Could it be that these bacteria consumers actually help the birds by reducing the abundance of pathogens?

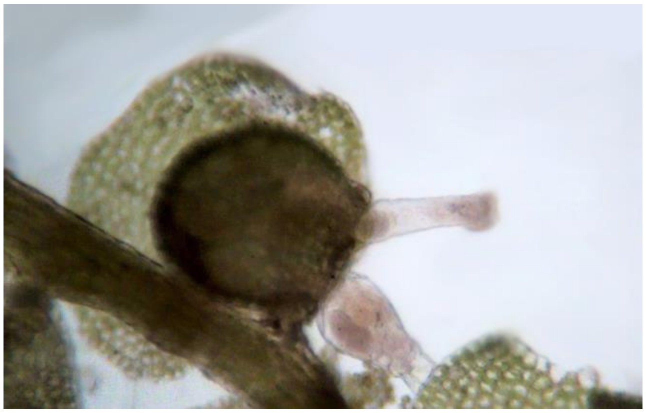

Figure 52. ***Frullania eboracensis*** lobule with rotifer. Photo courtesy of Lisa Pokorski.

We know that bryophytes themselves often have antibacterial properties (*e.g.* Basile *et al.* 1999; Alabrundzinska *et al.* 2003; Ariyo *et al*. 2011; Bukvicki *et al*. 2012; Asakawa *et al*. 2013; Yu *et al.* 2014), but until now, no study has demonstrated conclusively that they serve this purpose in the nests of birds.

At last, Fontúrbel *et al*. (2020) have shown that "Mamma knows best." They found that the hummingbird Picaflor Rubi (***Sephanoides sephaniodes***; Figure 53-Figure 54) selects the mosses ***Ancistrodes genuflexa*** (in 100% of the nests; Figure 55), ***Weymouthia mollis*** (27%; Figure 56), and ***Weymouthia cochlearifolia*** (17%; Figure 57) based on samples in austral South America, but ***A. genuflexa*** is particularly scarce in the forest while comprising up to 97% of the moss nesting material. They identified five compounds with antibacterial properties (Figure 58) in ***A. genuflexa***.

Figure 53. ***Sephanoides sephaniodes***, a hummingbird that uses ***Ancistrodes genuflexa*** selectively in its nests, giving the nests antibiotic properties. Photo by Felipe Bernala, through Creative Commons.

Figure 54. ***Sephanoides sephaniodes*** nest made with mosses. Photo by Diucón, through Creative Commons.

Figure 55. ***Ancistrodes genuflexa***, the most common moss in nests of Picaflor Rubi (***Sephanoides sephaniodes***). Photo by Felipe Osorio Zúñiga, with permission.

Figure 56. ***Weymouthia mollis***, a moss used in nests of Picaflor Rubi (***Sephanoides sephaniodes***). Photo by Juan Larrain, with permission

Figure 57. ***Weymouthia cochlearifolia***, a moss used in nests of Picaflor Rubi (***Sephanoides sephaniodes***). Photo by Juan Larrain, with permission.

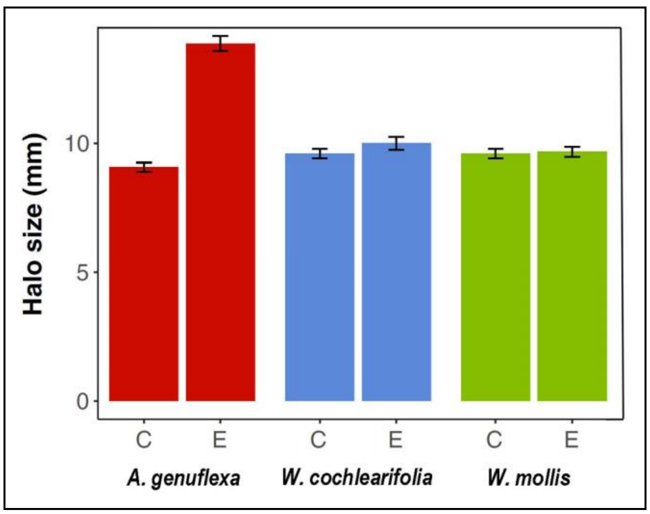

Figure 58. Antimicrobial activity of control (**C**) and moss extracts (**E**) from ***Ancistrodes genuflexa***, ***Weymouthia mollis***, and ***Weymouthia cochlearifolia***) against five common bacteria strands. Error bars represent standard error. Modified from Fontúrbel *et al*. 2020.

We know from other studies that birds may prefer materials that have antibiotic properties. Doctoral student Sarah Knutie became curious when one of Darwin's finches (Figure 59) pulled at cotton threads on the clothes line rope to use as nesting material (Pety 2020). She followed up with an experiment using cotton balls. Half of them had antibiotic solution (1% permethrin) and half had just water. These were available in wire-mesh dispensers. Of the 26 active nests examined, 85% contained cotton. Of these, 13 nests had permethrin-treated cotton and 9 had untreated cotton. Only 4 had no cotton. Of the 8 nests with at least 1 g of treated cotton, 7 had no parasites and the eighth had only 4. Hence, it appears that the birds may select materials with antibiotic properties. That could explain at least some of the selection of bryophytes for nesting material.

Figure 59. Darwin's finch with bryophytes in its beak, a bird that sometimes collects cotton balls with antibiotics for nesting. Photo by Rudy R., through Creative Commons.

There is a wide array of research projects needed to understand the role of bryophytes in nests. What is their elasticity compared to other nesting materials? Do they provide antibiotic properties that reduce parasites, fungi, or bacteria? Do they serve as better insulators than other materials? Do they keep the nest at a more constant humidity than other materials? Are they easier to work with or to carry than other materials?

Cavity Nest Elevation

Bryophytes have an additional function for cavity-nesting birds. They are often used to raise the nest cup so that the baby birds can be reached easily by the parents when feeding the birds and the birds can get in and out easily (Hamao *et al*. 2016). The bryophytes can also serve to separate the nest cups from cavity walls that may remain too moist, at the same time absorbing the excess moisture (Hamao *et al*. 2016).

Selection of Nest Materials

Just how choosy are the birds about the mosses they use? Breil and Moyle (1976) found that 11 birds had used 60 different species of mosses, including aquatic species, in their nests, suggesting that preference may simply depend on availability. Pant (1989) investigated the nests of five bird species in the Kumaon Himalaya and found that the primary mosses used were pleurocarpous. He supposed that these were preferred because they were easier to shape to suit the shape of the nest. This might also account for the use of larger leafy liverworts, in addition to pleurocarpous mosses, in the nest of the Streaked Laughing Thrush (***Trochalopteron lineatum***; Figure 60) (Pant & Tewari 1984). Furthermore, Abolina (1991) found that the large leafy liverworts ***Radula complanata*** (Figure 61) and ***Lophocolea heterophylla*** (Figure 62) were used for nesting material in Lithuania.

In their study of nests of twelve bird species, Breil and Moyle (1976) found that most birds chose the bryophytes that were most abundant locally. These included the aquatic mosses ***Fontinalis*** (Figure 63) and ***Hygrohypnum*** (Figure 64), and ***Sphagnum*** (Figure 16). Terrestrial mosses were mostly the pleurocarpous ***Brachythecium***

(Figure 65), ***Hedwigia*** (Figure 66), and ***Thuidium*** (Figure 67), plus the epiphytic bryophytes ***Frullania*** (Figure 30) and ***Platygyrium repens*** (Figure 68).

Figure 60. ***Trochalopteron lineatum***, Streaked Laughing Thrush, one of the few birds known to use leafy liverworts in its nest. Photo by P. Jeganathan, through Creative Common.

Figure 61. ***Radula complanata***, a nesting material for birds in Lithuania. Photo by Hermann Schachner, through Creative Commons.

Figure 62. ***Lophocolea heterophylla***, a nesting material for birds in Lithuania. Photo by Bob Klips, with permission.

Figure 63. ***Fontinalis antipyretica***; some members of this genus are used in bird nests. Photo by Andrew Spink, with permission.

Figure 64. ***Hygrohypnum ochraceum***, ; some members of this genus are used in bird nests. Photo by Michael Lüth, with permission.

Figure 65. ***Brachythecium rutabulum***, representing a genus commonly used in bird nests. Photo by Kristian Peters, through Creative Commons.

Figure 66. Dry ***Hedwigia ciliata*** with capsules, a pleurocarpous species commonly used in bird nests. Photo by Hugues Tinguy, through Creative Commons.

Figure 67. ***Thuidium delicatulum***, representing a genus commonly used in bird nests. Photo by Janice Glime.

Figure 68. ***Platygyrium repens***, an epiphytic moss commonly used in bird nests in the Appalachians, USA. Photo by Hermann Schachner, through Creative Commons.

Other birds appear to be especially choosy. In Hawaii, one bird nest (most likely of a non-native species) made its nest almost entirely from the setae and capsules of ***Pyrrhobryum*** (***Rhizogonium***) ***spiniforme*** (Figure 69-Figure 70) (Brandon Stone, Bryonet 9 April 2003).

Figure 69. ***Pyrrhobryum spiniforme***, a moss used exclusively in some bird nests in Hawaii. Photo by Alan Cressler, with permission.

Figure 70. ***Pyrrhobryum spiniforme*** with capsule and seta that are used for nests by some birds in Hawaii. Photo by Janice Glime.

In the Uluguru Mountains of Tanzania, Tamás Pócs (Bryonet 2 June 2010) observed a nest of a small bird made purely of ***Orthostichella rigida*** (Figure 71), a common hanging epiphyte.

Figure 71. ***Orthostichella rigida*** from Tasmania, a pendent moss used in bird nests there. Photo courtesy of Tamás Pócs.

In Kenya, Min Chuah Petiot (Bryonet 2 June 2010) has collected an abandoned and fallen nest made with the hanging moss ***Papillaria africana*** (Figure 72). This moss was still green and alive.

Figure 72. ***Papillaria africana***, nesting material in Kenya. Photo by Bruno Senterre, with permission.

Gustavo Tomás and Andrew Spink (Andrew Spink, Bryonet 2 June 2010) collected moss samples from a large number of Blue Tit (***Cyanistes caeruleus***; Figure 22) and Coal Tit (***Periparus ater***; Figure 73) nests from a woodland in the eastern Netherlands. The most common species in nests was ***Hypnum cupressiforme*** (Figure 74-Figure 75), which is common in the area. However, other locally common mosses were less common in the nests, indicating that the birds clearly selected certain species. It is interesting that different species were used in different parts (top/bottom) of the nest.

Figure 73. ***Periparus ater***, Coal Tit, a species that commonly uses ***Hypnum cupressiforme*** (Figure 74) in its nests in The Netherlands. Photo from Biopix, through Creative Commons.

Figure 74. ***Hypnum cupressiforme***, a moss commonly used in nests of Blue Tits and Coal Tits, covering the log. Photo by Michael Lüth, with permission.

Figure 75. ***Hypnum cupressiforme*** var ***cupressiforme***, a preferred moss in nests of Blue Tits and Coal Tits. Photo by David Holyoak, with permission.

In the Pacific Northwest of Oregon and Washington, all seven thrush species (**Turdidae**) and six hummingbird species (**Trocholidae**) use either bryophytes or lichens in their nests (Wolf 2009). All nine crows and jays (**Corvidae**) except the Black-billed Magpie (***Pica hudsonia***; Figure 76-Figure 77) use bryophytes for nesting material. These Pacific Northwest bryophytes include ***Alsia*** (Figure 78), ***Brachythecium*** (Figure 65), ***Calliergon*** (Figure 79), ***Dendroalsia*** (Figure 80), ***Dicranum*** (Figure 81), ***Eurhynchium*** (Figure 82), ***Homalothecium*** (Figure 83), ***Hypnum*** (Figure 74), ***Isothecium*** (Figure 84), ***Pogonatum*** (Figure 85), ***Pohlia*** (Figure 91), ***Polytrichum*** (Figure 86), ***Porella*** (Figure 88), and ***Sphagnum*** (Figure 87).

Figure 76. ***Pica hudsonia***, Black-billed Magpie, a bird that does not use bryophytes in its nest. Photo by Carplips, through Creative Commons.

Figure 77. ***Pica hudsonia***, Black-billed Magpie, nest showing mud and vegetable matter, but no bryophytes. Photo by Rich Mooney, through Creative Commons.

Figure 78. ***Alsia californica*** with capsules, a moss used in nests in the Pacific Northwest, USA. Photo by Paul Wilson, with permission.

Figure 79. ***Calliergon giganteum*** with ice, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Kristian Peters, through Creative Commons.

Figure 80. ***Dendroalsia abietina***, a species used commonly in bird nests in the Pacific Northwest, USA. Photo by Michael Lüth, with permission.

Figure 81. ***Dicranum scoparium***, one of the mosses available for use in bird nests in the Pacific Northwest, USA. Photo by J. C. Schou, through Creative Commons.

Figure 82. ***Eurhynchium praelongum***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Janice Glime.

Figure 83. ***Homalothecium sericeum***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Michael Lüth, with permission.

Figure 84. ***Isothecium myosuroides***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Dale Vitt, with permission.

Figure 85. ***Pogonatum urnigerum***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Janice Glime.

One commonality to surmise from these studies is that short, acrocarpous mosses are rarely used. In the first report of bryophytes in bird nests in Chin, Cao and Gao (1991) found only pleurocarps among the 18 species used. These were mostly hanging mosses in **Meteoriaceae** (Figure 71), **Pterobryaceae** (Figure 89), and **Trachypodaceae** (Figure 90). Mosses that are long, mostly pleurocarpous species or those with a **plagiotropic** (growing inclined or nearly horizontally) habit, and larger

leafy liverworts comprise almost all of the bryophytes in bird nests. (Most leafy liverworts grow horizontally.)

Figure 86. ***Polytrichum juniperinum***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Vincent de Boer, through Creative Commons.

Figure 87. ***Sphagnum fimbriatum***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by David T. Holyoak, with permission.

Figure 88. ***Porella navicularis***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Rosemary Taylor, with permission.

Figure 89. ***Pterobryon densum*** (**Pterobryaceae**), in one of the three most common bryophyte families in Chinese bird nests. Photo by Michael Lüth, with permission.

Figure 90. ***Bryowijkia ambigua*** (**Trachypodaceae**), in one of the three most common bryophyte families in Chinese bird nests. Photo by Li Zhang, with permission.

Even in the case of the acrocarpous moss ***Pohlia nutans*** (Figure 91) in a nest, it was only the sporophytes that were used (Crum 1973). Mrs. Cuthbert, of Mount Pleasant, Michigan, USA, reported that she found a bird nest lined with moss sporophytes (a hundred or so, as in Figure 92), giving a gold-colored look to the interior on a wet day (Crum 1973). Crum identified the moss as ***Pohlia nutans*** (Figure 91).

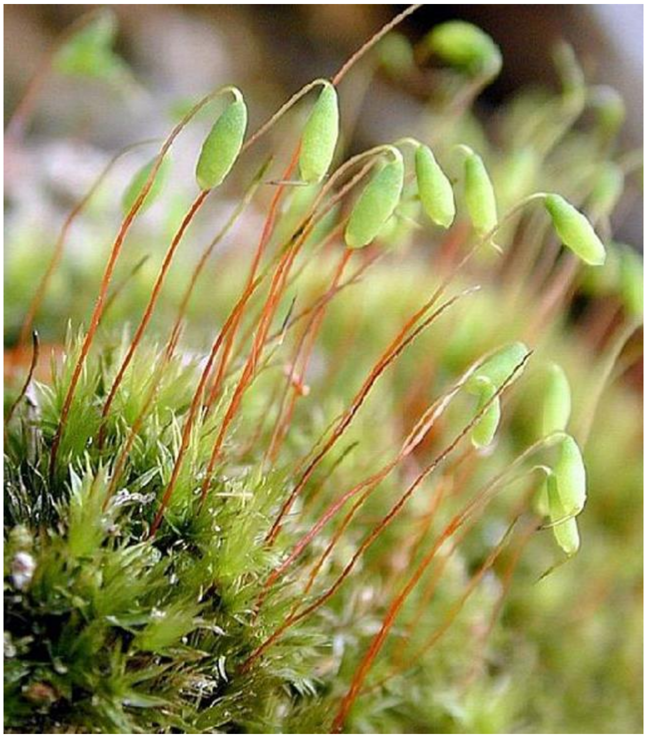

Figure 91. ***Pohlia nutans*** with capsules; setae of this moss are used in some bird nests. Photo by Michael Lüth, with permission.

Figure 92. Nest with sporophyte setae and capsules, possibly from ***Pohlia nutans*** (Figure 91). Photo courtesy of Lovatt.

Who Uses Mosses in Nests?

Breil and Moyle (1976) examined a number of nests of 12 eastern USA birds, identifying 65 species of mosses used in construction. They reported that all North American passerine birds use bryophytes in their nests, emphasizing the importance of bryophytes as an ecosystem component. These 65 species of bryophytes included 5 species of leafy liverworts. Of the nests examined, only the Indigo Bunting (***Passerina cyanea***; Figure 93) nest (Figure 94) lacked bryophytes.

Wolf (2009) conducted an extensive survey of bryophyte usage by birds in the Pacific Northwest (Oregon and Washington), USA. These are listed by orders, along with other records, in the following nest subchapters.

Figure 93. ***Passerina cyanea***, Indigo Bunting, on moss, although it did not include these in its nest in the eastern USA study. Photo by Steve Trynoski, with permission.

Figure 94. ***Passerina cyanea***, Indigo Bunting, nest with eggs, showing total lack of bryophytes. Photo by Richard Bonnett, through Creative Commons.

Summary

Birds often use bryophytes in their nests. This inclusion may help to maintain a safe temperature, to maintain suitable moisture, to prevent disease and parasitism, to provide a soft lining, to camouflage the nest, to permit the nest to expand as nestlings grow, and to help hold the nest together.

The use of bryophytes in nests is much more common among the **Passeriformes** (perching birds) than among the other orders of birds. Some birds are very specific in their choices, using only one or a few species when many are in the area. Most birds choose bryophytes with a plagiotropic growth habit and avoid acrocarpous mosses. Some select sporophytes, especially setae, to serve as nest linings.

What is clear is that we know little about the advantages that bryophytes may give birds when the bryophytes are included in the nests.

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